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Body shape diversification along the benthic–pelagic axis in marine fishes

S. T. Friedman, S. A. Price, K. A. Corn, O. Larouche, C. M. Martinez and P. C. Wainwright

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Review timeline
Original submission: 7 May 2020
Revised submission: 23 June 2020
Final acceptance: 29 June 2020

Note: Reports are unedited and appear as submitted by the referee. The review history appears in chronological order.

Review History

RSPB-2020-1053.R0 (Original submission)

Review form: Reviewer 1

Recommendation
Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Excellent

General interest: Is the paper of sufficient general interest?
Excellent

Quality of the paper: Is the overall quality of the paper suitable?
Good

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
The authors have added additional analyses to the manuscript and I find the methods/results to be compelling. I commend the authors on the amount of work they have done during revision and find most of the conclusions well justified.

However, I am perplexed by portions of the discussion and caution the authors against implementing such a narrow definition of convergence and the adaptive landscape in their study. The results of the study show that body and head depth is significantly smaller in pelagic versus demersal species, which is a strong result given the amount of morphological, ecological, and lineage diversity in the study. However, the authors spend much of the discussion downplaying these results as "weak" with no justification of why these significant results are "weak" or what strong results would look like. The authors seem to be hypothesizing that all pelagic fishes sit on one adaptive optimum, while all demersal fishes sit on another (Line 406) and that species invading the same habitat must evolve the same exact morphology. This is an unrealistic hypothesis given the diversity of morphological characters and lineages in this study.

I am wondering what the authors would expect the results to look like if adaptation to the pelagic environment selected for a more streamlined body shape and how do their results deviate from those predictions that make the results weak compared to other studies. I agree that lineages in demersal and pelagic habitats exhibit a variety of body shapes, but this makes the significant results even stronger than the results of previous studies.

The authors need to further justify their narrow interpretation of the adaptive landscape of fishes transitioning across the benthic(demersal)-habitat axis. Below I highlight sections that need further justification and interpretation.

Lines 216-218 and Table S2: In the results you state that head depth differed between pelagic-demersal habitats and body depth varied across all habitats. However, TableS2 shows the opposite.

Lines 282-286: Why is the signal weak? More justification is needed to define the significant result as weak, especially given the scale of this study.

Lines 286-292, 232-233, and 404-405: I am a bit confused by the interpretation here and the downplaying of the body/head depth results. The phyloANOVA/independent contrasts support the previous studies looking at morphological diversification across the benthic-pelagic habitat

axis. Your results show that body depth and head depth is significantly smaller in pelagic versus demersal species. This is a remarkably consistent result given the amount of species diversity, ecological variation, and evolutionary time separating many of these lineages. Basically, the two morphological characters that would be most expected to differ between pelagic and demersal habitats, differ in the direction predicted by the findings of the other 40 studies.

While I agree that there is more disparity in your dataset than if you looked at a single clade, would you really expect habitat adaptation to cause all of these diverse lineages to perfectly converge on the same morphotype? While you are not seeing perfect convergence, which I argue you would not expect at this scale, you are seeing similar changes in morphology during ecological convergence.

More justification is needed in the discussion to support this interpretation.

Lines 290-292: What is your definition of convergence here? Many authors would argue that parallel morphological changes away from sister groups that results in similar changes is a type of convergence. See Stayton 2006 Figure 3.

More justification is needed for why you do not consider this to be evidence of convergence.

Stayton 2006. Testing Hypotheses of Convergence with Multivariate Data: Morphological and Functional Convergence among Herbivorous Lizards. Evlolution 60(4): 824-841.

Line 383-385: A significant difference in body and head depth at this scale is much more surprising than a non-significant result. I do not understand why you downplay these results as "weak" or "slight". As mentioned in previous comments I think you need to do a better job of justifying why you think these significant results are weak.

Line 385-387: I strongly agree with this interpretation, but it appears to be at odds with other portions of the discussion where you downplay the significance of the morphological difference between demersal and pelagic fishes. I think this interpretation should feature more prominently in the discussion.

Line 406: This seems like a "straw man" argument. Does the literature really predict a narrow adaptive landscape for marine teleosts? It seems unlikely that anyone would expect one of the most diverse vertebrate radiations to exhibit a narrow adaptive landscape across multiple morphological characters that are influenced by multiple different ecological pressures.

Review form: Reviewer 2

Recommendation
Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Excellent

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Good

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
No

Do you have any ethical concerns with this paper?
No

Comments to the Author
Freidman et al. have presented a revised manuscript on the macroevolution morphological evolution associated with benthic/pelagic habitat shifts. I found the revised manuscript to be vastly improved. The added analyses provide some missing clarity on the role of phylogenetic scale in their results and increases the broader relevance beyond expecting clear patterns between these two or three habitat types. The discussion now has some teeth and better highlights the interesting aspects of their results.

I have no major suggestions and thank the authors for taking all the reviewer and editor comments very seriously. Congrats on a nice study.

I strongly suggest making the R code available. Why don't we all do this? Let's not gate keep and improve study replicability by making code available.

Line 180 – comma needed after "additionally"
Line 264 – I would suggest stating the difference between the BM1 and BMS model again here. Nearly every reader not working with these models every day will be forced to flip back and search the methods for the explanation. Help the reader out and use the same wording again here.

Decision letter (RSPB-2020-1053.R0)

11-Jun-2020

Dear Miss Friedman:

Your manuscript has now been peer reviewed and the reviews have been assessed by an Associate Editor. The reviewers' comments (not including confidential comments to the Editor) and the comments from the Associate Editor are included at the end of this email for your reference. The referees and Associate Editor were generally quite happy with the modifications of you manuscript. However, there are still a few remaining items that need to be addressed before you paper is ready for publciation.

Please modify your mansucript to deal with the few remaining issues. To submit your revision please log into http://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions", click on "Create a Revision". Your manuscript number has been appended to denote a revision.

When submitting your revision please upload a file under "Response to Referees" - in the "File Upload" section. This should document, point by point, how you have responded to the reviewers' and Editors' comments, and the adjustments you have made to the manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

Your main manuscript should be submitted as a text file (doc, txt, rtf or tex), not a PDF. Your figures should be submitted as separate files and not included within the main manuscript file.

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If your study uses animals please include details in the methods section of any approval and licences given to carry out the study and include full details of how animal welfare standards were ensured. Field studies should be conducted in accordance with local legislation; please include details of the appropriate permission and licences that you obtained to carry out the field work.

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It is a condition of publication that you make available the data and research materials supporting the results in the article. Datasets should be deposited in an appropriate publicly available repository and details of the associated accession number, link or DOI to the datasets must be included in the Data Accessibility section of the article (https://royalsociety.org/journals/ethics-policies/data-sharing-mining/). Reference(s) to datasets should also be included in the reference list of the article with DOIs (where available).

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should also be fully cited and listed in the references.

If you wish to submit your data to Dryad (http://datadryad.org/) and have not already done so you can submit your data via this link
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Electronic supplementary material:
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Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

Please submit a copy of your revised paper within three weeks. If we do not hear from you within this time your manuscript will be rejected. If you are unable to meet this deadline please let us know as soon as possible, as we may be able to grant a short extension.

Thank you for submitting your manuscript to Proceedings B; we look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Best wishes,
Dr Daniel Costa
mailto: proceedingsb@royalsociety.org

Associate Editor
Board Member: 1
Comments to Author:
I've received detailed reports from two of the referees who assessed the first submission and recommended major revisions or rejections. I commend the authors for taking the time to revise the paper thoroughly and for conducting additional analyses. Both referees now recommend "accept with minor revision."

Referee 1 has now made important comments on the interpretation of the results, while Referee 2 points to the importance of making the R code used in the analysis publicly available. I'm also not entirely convinced myself with the justification provided on my initial comment on habitat coding ambiguity. I wasn't referring to uncertainties associated with the reconstructions, but rather on how 100% of the species are assigned to different habitat categories with 100% certainty (as evidenced in new Table S1). Realistically, I'd expect to see in Table S1 instances of species with ambiguous habitat coding (e.g., benthic/demersal, or demersal/pelagic). The main text or the supplement should also include sensitivity analyses that test the extent to which these ambiguities affect the reconstructions and ultimately the interpretations. Minimally, some discussion on this is warranted.

Congratulations on an excellent paper! I look forward to seeing it published in Proc. B.

Sincerely,
Ricardo Betancur

Associate Editor

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)
The authors have added additional analyses to the manuscript and I find the methods/results to be compelling. I commend the authors on the amount of work they have done during revision and find most of the conclusions well justified.

However, I am perplexed by portions of the discussion and caution the authors against implementing such a narrow definition of convergence and the adaptive landscape in their study. The results of the study show that body and head depth is significantly smaller in pelagic versus demersal species, which is a strong result given the amount of morphological, ecological, and lineage diversity in the study. However, the authors spend much of the discussion downplaying these results as "weak" with no justification of why these significant results are "weak" or what strong results would look like. The authors seem to be hypothesizing that all pelagic fishes sit on one adaptive optimum, while all demersal fishes sit on another (Line 406) and that species invading the same habitat must evolve the same exact morphology. This is an unrealistic hypothesis given the diversity of morphological characters and lineages in this study.

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While I agree that there is more disparity in your dataset than if you looked at a single clade, would you really expect habitat adaptation to cause all of these diverse lineages to perfectly converge on the same morphotype? While you are not seeing perfect convergence, which I argue you would not expect at this scale, you are seeing similar changes in morphology during ecological convergence.

More justification is needed in the discussion to support this interpretation.

Lines 290-292: What is your definition of convergence here? Many authors would argue that parallel morphological changes away from sister groups that results in similar changes is a type of convergence. See Stayton 2006 Figure 3.

More justification is needed for why you do not consider this to be evidence of convergence.

Stayton 2006. Testing Hypotheses of Convergence with Multivariate Data: Morphological and Functional Convergence among Herbivorous Lizards. Evlolution 60(4): 824-841.

Line 383-385: A significant difference in body and head depth at this scale is much more surprising than a non-significant result. I do not understand why you downplay these results as "weak" or "slight". As mentioned in previous comments I think you need to do a better job of justifying why you think these significant results are weak.

Line 385-387: I strongly agree with this interpretation, but it appears to be at odds with other portions of the discussion where you downplay the significance of the morphological difference between demersal and pelagic fishes. I think this interpretation should feature more prominently in the discussion.

Line 406: This seems like a "straw man" argument. Does the literature really predict a narrow adaptive landscape for marine teleosts? It seems unlikely that anyone would expect one of the most diverse vertebrate radiations to exhibit a narrow adaptive landscape across multiple morphological characters that are influenced by multiple different ecological pressures.

Referee: 2

Comments to the Author(s)
Freidman et al. have presented a revised manuscript on the macroevolution morphological evolution associated with benthic/pelagic habitat shifts. I found the revised manuscript to be vastly improved. The added analyses provide some missing clarity on the role of phylogenetic scale in their results and increases the broader relevance beyond expecting clear patterns between these two or three habitat types. The discussion now has some teeth and better highlights the interesting aspects of their results.

I have no major suggestions and thank the authors for taking all the reviewer and editor comments very seriously. Congrats on a nice study.

I strongly suggest making the R code available. Why don't we all do this? Let's not gate keep and improve study replicability by making code available.

Line 180 – comma needed after "additionally"
Line 264 – I would suggest stating the difference between the BM1 and BMS model again here. Nearly every reader not working with these models every day will be forced to flip back and search the methods for the explanation. Help the reader out and use the same wording again here.

Author's Response to Decision Letter for (RSPB-2020-1053.R0)

See Appendix A.

Decision letter (RSPB-2020-1053.R1)

29-Jun-2020

Dear Miss Friedman

I am pleased to inform you that your manuscript entitled "Body shape diversification along the benthic-pelagic axis in marine fishes" has been accepted for publication in Proceedings B.

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

If you are likely to be away from e-mail contact please let us know. Due to rapid publication and an extremely tight schedule, if comments are not received, we may publish the paper as it stands.

If you have any queries regarding the production of your final article or the publication date please contact procb_proofs@royalsociety.org

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Electronic supplementary material:
All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,

Dr Daniel Costa
Editor, Proceedings B
mailto: proceedingsb@royalsociety.org

Appendix A

Responses to Reviewers

I'm also not entirely convinced myself with the justification provided on my initial comment on habitat coding ambiguity. I wasn't referring to uncertainties associated with the reconstructions, but rather on how 100% of the species are assigned to different habitat categories with 100% certainty (as evidenced in new Table S1). Realistically, I'd expect to see in Table S1 instances of species with ambiguous habitat coding (e.g., benthic/demersal, or demersal/pelagic). The main text or the supplement should also include sensitivity analyses that test the extent to which these ambiguities affect the reconstructions and ultimately the interpretations. Minimally, some discussion on this is warranted.

We thank the editor for this feedback and fully agree that transparency as to limitations of our habitat codings are warranted. In response to this comment, we have added a brief discussion of the issue to the manuscript (Lines 397-402). We do not perform full sensitivity analyses of ambiguity in habitat codings because we do not feel that it is realistic to objectively assess the level of ambiguity in these codings, whether due to flexible or variable habitat use by some species, limitations to knowledge of habitat use, or errors in the literature. We reiterate that we have no reason to believe there is any bias in the habitat codings that would have a substantial effect on the general patterns found in this study. Nevertheless, we agree that it is important to be explicit about our inability to account for uncertainty with respect to habitat.

Referee 1

I am perplexed by portions of the discussion and caution the authors against implementing such a narrow definition of convergence and the adaptive landscape in their study. The results of the study show that body and head depth is significantly smaller in pelagic versus demersal species, which is a strong result given the amount of morphological, ecological, and lineage diversity in the study. However, the authors spend much of the discussion downplaying these results as "weak" with no justification of why these significant results are "weak" or what strong results would look like. The authors seem to be hypothesizing that all pelagic fishes sit on one adaptive optimum, while all demersal fishes sit on another (Line 406) and that species invading the same habitat must evolve the same exact morphology. This is an unrealistic hypothesis given the diversity of morphological characters and lineages in this study.

We thank the reviewer for their thoughtful feedback. As there are few studies of morphological evolution on this scale, it is difficult to know at what point results are biologically significant or even what the expectation of a "strong" effect would look like, considering the vast ecological and phylogenetic diversity contained in this dataset. We erred on the side of caution in interpreting our results, however we agree that our discussion, as it is currently written, downplays key results in this study too much. In response to the comments, we have removed the terminology that refers to our results as weak or subtle. We have also featured our positive results regarding consistent trait changes more prominently and earlier in the discussion. Furthermore, we agree that the expectation that there is a single adaptive optimum for each habitat is unrealistic, especially for a dataset encompassing such a large swath of teleost diversity. In response, we have removed any references to a narrow adaptive landscape and

instead emphasize that the morphological diversification we find is an expected outcome given the macroevolutionary nature of this dataset.

I am wondering what the authors would expect the results to look like if adaptation to the pelagic environment selected for a more streamlined body shape and how do their results deviate from those predictions that make the results weak compared to other studies. I agree that lineages in demersal and pelagic habitats exhibit a variety of body shapes, but this makes the significant results even stronger than the results of previous studies.

Again, the reviewer makes a good point about how we should expect to see the habitat effect superimposed upon extensive diversification within habitat. Please see our response above. We no longer refer to our results as weak.

The authors need to further justify their narrow interpretation of the adaptive landscape of fishes transitioning across the benthic(demersal)-habitat axis. Below I highlight sections that need further justification and interpretation.

Please see our response above. We no longer refer to fishes as having a narrow adaptive landscape.

Lines 216-218 and Table S2: In the results you state that head depth differed between pelagic-demersal habitats and body depth varied across all habitats. However, Table S2 shows the opposite.

We thank the reviewer for their careful reading of the manuscript. We had mistakenly switched our results for maximum body depth and head depth in the text of our manuscript. We have fixed the issue now.

Lines 282-286: Why is the signal weak? More justification is needed to define the significant result as weak, especially given the scale of this study.

We have rephrased this sentence and no longer refer to the signal as weak.

Lines 286-292, 232-233, and 404-405: I am a bit confused by the interpretation here and the downplaying of the body/head depth results. The phyloANOVA/independent contrasts support the previous studies looking at morphological diversification across the benthic-pelagic habitat axis. Your results show that body depth and head depth is significantly smaller in pelagic versus demersal species. This is a remarkably consistent result given the amount of species diversity, ecological variation, and evolutionary time separating many of these lineages. Basically, the two morphological characters that would be most expected to differ between pelagic and demersal habitats, differ in the direction predicted by the findings of the other 40 studies.

Please see our response above. We have rephrased the manuscript in multiple locations to emphasize our positive results instead of downplaying them.

While I agree that there is more disparity in your dataset than if you looked at a single clade, would you really expect habitat adaptation to cause all of these diverse lineages to perfectly converge on the same morphotype? While you are not seeing perfect convergence, which I argue you would not expect at this scale, you are seeing similar changes in morphology during ecological convergence. More justification is needed in the discussion to support this interpretation.

We completely agree with this feedback. Please see our response above. We have rephrased the manuscript in multiple locations to emphasize our positive results instead of downplaying them.

Lines 290-292: What is your definition of convergence here? Many authors would argue that parallel morphological changes away from sister groups that results in similar changes is a type of convergence. See Stayton 2006 Figure 3. More justification is needed for why you do not consider this to be evidence of convergence.

Although we agree that the patterns we find here might indicate morphological convergence, we have not quantified convergence in this study and thus feel uncomfortable making such claims. Furthermore, were we to run such analysis on this dataset, we are not likely to find a significant signal of convergence. As the reviewer has stated (and we agree) there is no expectation of a narrow adaptive landscape across a dataset that encompasses such ecological and phylogenetic diversity. In an effort to address this comment, we have now removed this sentence as well as any explicit reference to convergence and instead focus on our ability to recover consistent morphological signal aligning with the expectations in the literature.

Line 383-385: A significant difference in body and head depth at this scale is much more surprising than a non-significant result. I do not understand why you downplay these results as "weak" or "slight". As mentioned in previous comments I think you need to do a better job of justifying why you think these significant results are weak.

We have changed the phrasing of this sentence and no longer refer to our results as weak or slight.

Line 385-387: I strongly agree with this interpretation, but it appears to be at odds with other portions of the discussion where you downplay the significance of the morphological difference between demersal and pelagic fishes. I think this interpretation should feature more prominently in the discussion.

We have moved this sentence earlier in our discussion and now elaborate on it in an effort to feature this interpretation more prominently. We no longer downplay the significance of the morphological differences between demersal and pelagic fishes.

Line 406: This seems like a “straw man” argument. Does the literature really predict a narrow adaptive landscape for marine teleosts? It seems unlikely that anyone would expect one of the most diverse vertebrate radiations to exhibit a narrow adaptive landscape across multiple morphological characters that are influenced by multiple different ecological pressures.

We agree with this comment and no longer refer to an expectation of a narrow adaptive landscape in the manuscript.

Referee 2

I strongly suggest making the R code available. Why don't we all do this? Let's not gate keep and improve study replicability by making code available.

We completely agree that code should be made readily available. STF has already added the function for our additional PIC analysis to her public GitHub repository. However, in response to this comment, we have added this function, as well as the code we used to implement the PIC analysis for this study to the associated Dryad repository. All other analyses for this study involved using openly available R functions detailed throughout the manuscript.

Line 180 – comma needed after “additionally”

We have made the requested change.

Line 264 – I would suggest stating the difference between the BM1 and BMS model again here. Nearly every reader not working with these models every day will be forced to flip back and search the methods for the explanation. Help the reader out and use the same wording again here.

We thank the reviewer for this feedback and have clarified the major difference between the two models in this section.